

## Dynamics and composition of litterfall in an unmanaged Norway spruce (*Picea abies*) forest after bark-beetle outbreak

Jiří Kopáček<sup>1)2)\*</sup>, Pavel Cudlín<sup>3)</sup>, Hana Fluksová<sup>2)</sup>, Jiří Kaňa<sup>1)</sup>, Tomáš Pícek<sup>2)</sup>, Hana Šantrůčková<sup>2)</sup>, Miroslav Svoboda<sup>4)</sup> and Daniel Vaněk<sup>2)</sup>

<sup>1)</sup> Biology Centre AS CR, Institute of Hydrobiology, Na Sádkách 7, CZ-37005 České Budějovice, Czech Republic (\*corresponding author's e-mail: jkopacek@hbu.cas.cz)

<sup>2)</sup> Faculty of Science, University of South Bohemia, Branišovská 31, CZ-37005 České Budějovice, Czech Republic

<sup>3)</sup> Institute of Systems Biology and Ecology, AS CR, Na Sádkách 7, CZ-37005 České Budějovice, Czech Republic

<sup>4)</sup> Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 129, CZ-16521 Prague, Czech Republic

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We investigated litterfall chemistry and fluxes, and cellulose decomposition in litter floor in mature, unmanaged Norway spruce stands in the catchments of Plešné and Čertovo lakes (Czech Republic) during 2003–2013. The Plešné forest was infested by the bark beetle (*Ips typographus*) in 2004, and 88%–99% of trees had died by 2011. Total litterfall and its composition were similar in both catchments in 2003. The litterfall increased from 5.4 to 42 t ha<sup>-1</sup> yr<sup>-1</sup> after the infestation and remained relatively high (5.0 t ha<sup>-1</sup> yr<sup>-1</sup>) until the end of the study even though > 52% of trees were already broken. The chemical composition of most spruce litter categories changed after infestation, with the most pronounced trends in C (decrease) and Ca (increase) concentrations. Moreover, Mg, K, and P concentrations increased in the total Plešné litter due to an increasing proportion of rowan litter. Cellulose decomposition increased in the litter floor after infestation.

### Introduction

Factors associated with climate change including increasing temperature, drought, and windthrow frequency have increased the susceptibility of forests to insect attacks, and already contribute to large-scale tree mortalities in numerous regions in Europe, North America, and Asia (Huber *et al.* 2004a, Tokuchi *et al.* 2004, Raffa *et al.* 2008, Mikkelsen *et al.* 2013a, 2013b).

Microclimate, hydrology, and biogeochemical cycles of many elements are significantly altered in the insect-infested and damaged forests. The amounts of bioavailable fresh organic matter (litter, dead roots and aboveground tree parts) abruptly increase on the forest floor and in upper soil horizons. Moreover, reduced canopy shading and lower transpiration result in elevated soil temperature and moisture (Hais and Kučera 2008, Mikkelsen *et al.* 2013a). These changes,

following forest dieback after insect attacks, promote a series of sequential and parallel changes in soil microbial processes similar to other types of forest disturbances (e.g., windthrows and clearcuts). In addition to elevated mineralization and nitrification in soils (e.g., Huber *et al.* 2004a, 2004b), the reduction or cessation of supplies of energy-rich plant assimilates from dead trees to mycorrhizal fungal symbionts reduces the biomass of mycorrhizal fungi and causes changes in soil microbial communities (Högberg *et al.* 2007), and alters carbon (C) and nitrogen (N) cycling in soils (Kopáček *et al.* 2013a). These changes govern or affect the pre-disturbance cycles of other elements, resulting in the following changes in soil and water composition compared to undisturbed ecosystems: (1) The elevated availability of inorganic N in soils is manifested by increased  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations in soil solutions and increased  $\text{NO}_3^-$  leaching (Huber *et al.* 2004a, 2004b, Tahovská *et al.* 2010). (2) The elevated concentrations of  $\text{NO}_3^-$  in soil solutions mobilize  $\text{H}^+$ , base cations [potassium (K), magnesium (Mg), and calcium (Ca)] liberated from decaying tissue, and aluminium (Al) liberated from the soil sorption complex (Berdén *et al.* 1997, Swank *et al.* 2001, Finér *et al.* 2003, Houlton *et al.* 2003, Burns and Murdoch 2005, McHale *et al.* 2007, Kaňa *et al.* 2013). (3) Decomposition of the fresh litter and fine roots in soils, the lack of nutrient uptake by dead trees, and altered microbial functioning contribute to elevated leaching of inorganic and organic phosphorus (P) forms and dissolved organic C and N (Adamson and Hornung 1990, Ahtiainen and Huttunen 1999, Piirainen *et al.* 2002, 2004, Mikkelsen *et al.* 2013a, 2013b). (4) Continuous liberation of base cations from dead biomass left in unmanaged stands contributes to an increase in soil base saturation (Kaňa *et al.* 2013) and mitigates pH declines in surface waters after the forest dieback (Kopáček *et al.* 2013b).

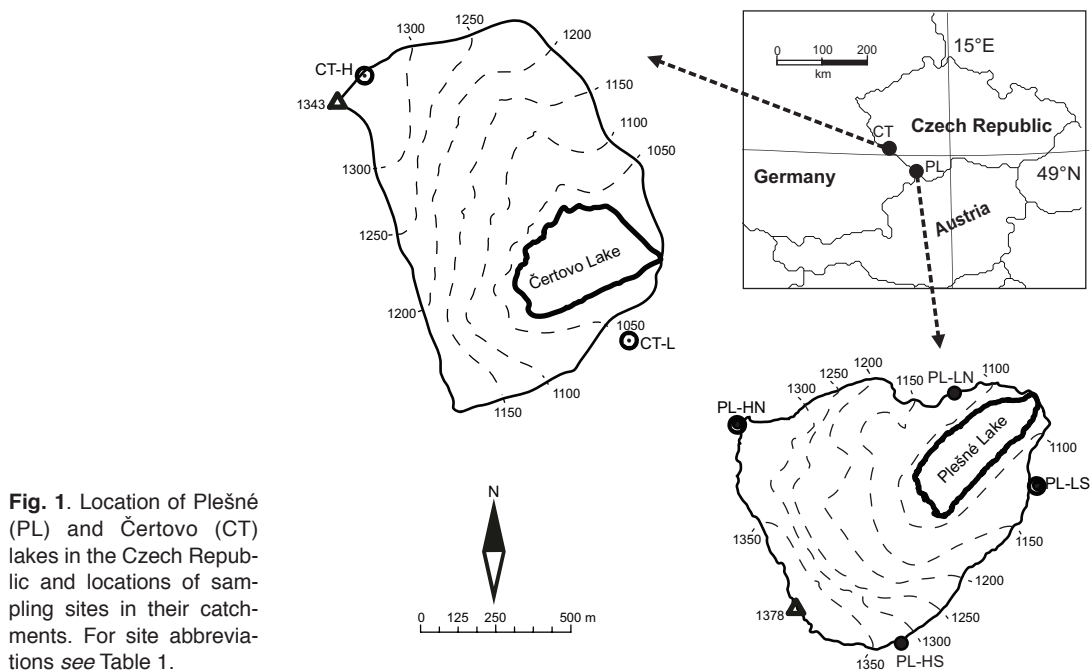
Studies on ecosystem changes associated with forest dieback caused by insect attacks usually begin after a bark-beetle outbreak, and data on the dynamics of forest decay prior to and during bark-beetle infestations are still lacking. Such a dynamic may represent an important ecosystem factor, controlling nutrient inputs to

the forest floor and, consequently, the rapidity and duration of biogeochemical changes in soils and the chemistry of receiving waters. As part of long-term ecological research of boreal forest catchment-lake ecosystems of Plešné and Čertovo lakes in the Bohemian Forest (south-western Czech Republic), forest status (Svoboda *et al.* 2006a, 2006b, 2006c), litterfall fluxes and chemistry (Kopáček *et al.* 2010), and cellulose decomposition (H. Šantrůčková unpubl. data) have been studied since the early 2000s. Even though the stands differ in bedrock, soil base saturation, and N saturation, chemical composition of their litter and foliage differ significantly only in Ca and N concentrations (Kopáček *et al.* 2010). Catchment of Plešné Lake has been affected by bark-beetle infestation and forest dieback since 2004. The relatively small between catchment differences in litter chemistry and pre-disturbance records in the affected catchment provided us a unique opportunity to compare changes in litterfall dynamics and chemical composition in disturbed vs. undisturbed stands in the same area. The aim of our study was to evaluate (i) litterfall dynamic and chemistry prior to, during, and after bark-beetle infestation and forest dieback and (ii) the effect of forest disturbance on decomposition rate of cellulose in the litter floor.

## Material and methods

### Study site description

The Bohemian Forest catchments of Plešné (PL) and Čertovo (CT) lakes are situated at elevations between 1030 and 1378 m a.s.l., and are north-east- and east-oriented, respectively (Fig. 1). Bedrock is formed by granite (relatively rich in P and Ca) and mica-schist in the PL and CT catchments, respectively. Soils in both catchments are mostly leptosol, podsol and dystic cambisol, and are shallower (33 vs. 65 cm), but with higher base saturation (15% vs. 9%), in the PL than CT catchment (Kopáček *et al.* 2002a, 2002b). According to the updated climate classification (Peel *et al.* 2007), the study area belongs to the Dfc category, i.e. cold climate, with monthly average air temperature exceeding



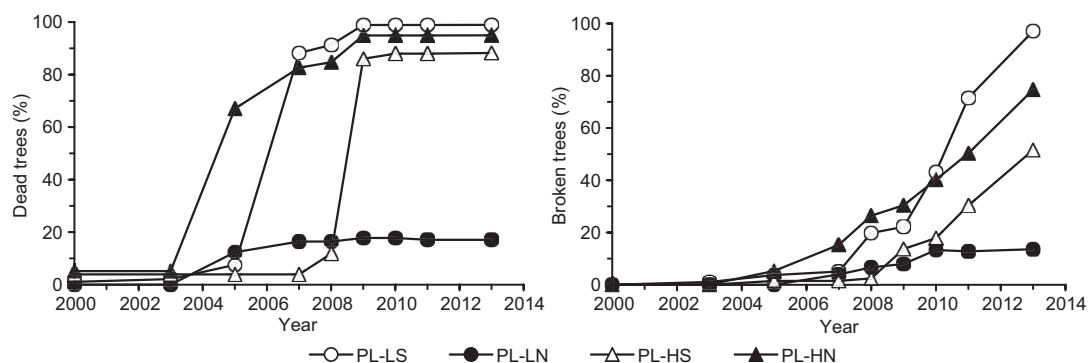
**Fig. 1.** Location of Plešné (PL) and Čertovo (CT) lakes in the Czech Republic and locations of sampling sites in their catchments. For site abbreviations see Table 1.

10 °C only in three summer months (Turek *et al.* 2014). Present annual average air temperatures and precipitation at the elevation of ~1100 m are ~4.7 °C and ~1200 mm, respectively (Kopáček *et al.* 2011, Turek *et al.* 2014). At the beginning of the study, both catchments were covered with mature (mostly > 150 years old) forests, dominated by Norway spruce (*Picea abies*), with a minor contribution of European beech (*Fagus sylvatica*), silver fir (*Abies alba*), birch (*Betula pubescens* and *B. pendula*), and rowan (*Sorbus aucuparia*). For more details on understory vegetation, soil and precipitation see Svoboda *et al.* (2006a) and Kopáček *et al.* (2010, 2011). Recent studies show that severe natural disturbances were a common part of natural dynamics of Norway spruce stands in the Bohemian Forests during the last three centuries (Svoboda *et al.* 2012, Čada *et al.* 2013).

This study was conducted at four research plots in the PL catchment and two plots in the CT catchment (Table 1). One PL plot (PL-LS) was located at low (L) elevation (1122 m), and two others (PL-HS and PL-HN) at high (H) elevations (1313 and 1334 m); abbreviations S (south) and N (north) denote the plot position in the PL catchment (Fig. 1). Plots CT-L and CT-H were located at low (1057 m) and high (1330 m) eleva-

tions, respectively, in the CT catchment (Fig. 1). All these plots have been in existence since June 2003. After the forest dieback in the PL catchment (*see below*) in June 2008, we established an additional plot, PL-LN, in the only part of the PL catchment that was not seriously affected by bark-beetle infestation at a similar elevation as the affected PL-LS plot (Table 1). All plots were located in flat areas in mature Norway spruce forests, with a small proportion of beech at CT-L and an increasing proportion of rowan at PL-HN (since 2010). The forest at the additional PL-LN plot was formed by a mixture of mature and young trees with a dominance of Norway spruce and a small proportion of rowan and birch. During the study, the annual average air temperature and throughfall precipitation at the individual plots ranged from 3.8–5.5 °C and 1188–1595 mm, respectively (Table 1), and snow cover usually lasted 5–6 months during November–April.

The areal densities of healthy, dead (bark-beetle attacked), and broken trees were calculated at each plot using colour aerial photographs (scales 1:5000–7000), prepared by Argus Geo System Ltd. (Hradec Králové, Czech Republic) and Georeal (Plzeň, Czech Republic) in 2000, 2003, 2005, 2007–2011, and 2013. Calculations were done for 1 ha circular areas (except for PL-LN;



**Fig. 2.** Time series of the proportions of dead and broken trees at the plots in the Plešné (PL) catchment. For site abbreviations see Table 1.

only 0.13 ha due to only a small area of surviving forest), with centres in the middle of the plots. The data were verified by a field survey in the CT catchment (M. Svoboda unpubl. data). At the individual PL and CT plots, the number of living Norway spruce trees in 2003 varied between 374 and 776 ha<sup>-1</sup> (Table 1). Trees at all plots were partly damaged by a windstorm (broken canopies, branches, a high amount of twigs in litterfall) in the winters of 2005, 2007, and 2008 (Kopáček *et al.* 2010). The plots PL-HN, PL-LS, and PL-HS were affected by the bark beetle (*Ips typographus*) in 2004, 2006, and 2008, respectively, and 88%–99% of Norway spruce trees were already dead at these plots in 2011 (Fig. 2). The dead trees were continuously broken by winds, and 97%, 75% and 52% of the trees present when the study had begun were already broken in 2013 at the PL-LS, PL-HN, and PL-HS plots, respectively. The CT-L and CT-H plots

were less affected than the PL plots, with ~6% and 23% of vigorous trees broken by windstorms between 2003 and 2013 (Table 1), but with a negligible contribution of bark-beetle outbreak. No tree located above the samplers died at the CT-L, CT-H, and PL-LN plots during the study.

### Litter sampling and analyses

Litter was sampled using 5 square frame traps [80 × 80 cm, height of 15 cm, bottom made of plastic net (mesh size < 0.2 mm)] situated at each plot beneath five representative trees (typical age, height, diameter, and crown status at the plot and surrounding area) from June 2003 to May 2013. Litter was collected three times per year, in spring after snowmelt at the upper plots (mostly at the end of May), in August, and between late October and early November. Litter from each

**Table 1.** Locations of plots with litter traps in the catchments of Plešné (PL) and Čertovo (CT) lakes in the Bohemian Forest. Abbreviations: L, low elevation; H, high elevation; S, south; N, north; ND, not determined.

	PL-LS	PL-LN	PL-HS	PL-HN	CT-L	CT-H
Latitude (°N, WGS-84)	48.7752	48.7776	48.7700	48.7767	49.1627	49.1696
Longitude (°E, WGS-84)	13.8680	13.8642	13.8630	13.8547	13.1993	13.1858
Elevation (m a.s.l.)	1122	1115	1313	1334	1057	1330
Living trees in 2003 (number per ha)	646	479	408	776	472	374
Dead trees in 2003/2013 (%)	2/99	0/17	4/88	5/95	3/10	7/30
Operated from (month/year)	VI/2003	V/2008	VI/2003	VI/2003	VI/2003	VI/2003
Annual precipitation <sup>1</sup> (mm)	1188	ND	ND	1383	1242	1595
Air temperature <sup>1</sup> (°C)	5.5	ND	ND	4.1	5.3	3.8

<sup>1</sup>) Annual averages of precipitation amount (throughfall) and air temperature (based on hourly records) during June 2003 to June 2013 (Turek *et al.* 2014).

trap was collected individually and separated into the following six categories: needles, twigs, bark, lichen, cones, and “other material”, i.e., remaining material, consisting mostly of poorly identifiable fragments. Beech leaves formed another category at CT-L, the only study plot where beech trees occurred. Another four categories, birch and rowan leaves and twigs were collected at PL-LN during 2008–2013. Rowan leaves and twigs were also collected at the PL-HN plot since rowan began to occur at this plot in 2010. Each fraction was dried at 50 °C for 12 hours. Samples from the August and autumn samplings were combined to obtain one sample representing the summer–autumn period.

For chemical analyses, the dry samples of each category from all five traps were combined into one integrated sample for each plot, homogenised, and 2–5 g subsamples were finely ground for chemical analyses. Dry weight (DW) and ash content were obtained by drying at 105 °C for 2 hours and combustion at 550 °C for 2 hours in an oven, respectively. Total P was determined by  $\text{HNO}_3$  and  $\text{HClO}_4$  digestion according to Kopáček *et al.* (2001). Total carbon (C) and N were determined by a CN analyzer (NC 2100, ThermoQuest, Italy) according to Nelson and Sommers (1996). Total concentration of metals (Ca, Mg, Na, K, Al, Fe, and Mn) was determined by flame atomic absorption spectrometry after mineralization ( $\text{HNO}_3$ ,  $\text{H}_2\text{SO}_4$ , and HF; at 200 °C for 2 hours) in the accredited laboratory of the Czech Geological Survey, Prague. The original method (Emteryd 1989) was modified as follows: 1.0 g of sample was used instead of 0.4 g and  $\text{HClO}_4$  was replaced by  $\text{H}_2\text{SO}_4$ . The reliability of the analytical results was controlled by means of a standard sample (finely ground spruce needles) that was assayed with each series of samples. The average ( $\pm$  SD) element concentrations in this control sample (number of analyses,  $n = 22$ ) were ( $\mu\text{mol g}^{-1}$ ): 43 560 ( $\pm$  712) for C, 921 ( $\pm$  36) for N, 26 ( $\pm$  0.9) for P, 97 ( $\pm$  7.3) for Ca, 18 ( $\pm$  1.2) for Mg, 1.4 ( $\pm$  0.6) for Na, 32 ( $\pm$  1.8) for K, 4.4 ( $\pm$  0.3) for Al, 1.3 ( $\pm$  0.2) for Fe, and 4.8 ( $\pm$  0.2) for Mn. No element in the control sample exhibited a significant concentration trend during the study.

All analyses were performed with samples dried at 50 °C, but chemical results further

reported in this study were recalculated per the DW. The annual average composition of samples is based on samples collected during summer (June–October) and winter (November–May), i.e. between the consecutive spring samplings.

The chemical composition of foliage (sampled in 2001; Kopáček *et al.* 2010) and fine branches (diameter < 5 mm) and bark (sampled in 2003; Svoboda *et al.* 2006b), representing the situation prior to bark-beetle infestation, was determined by the same methods and laboratories as litter. Data on element pools in the PL and CT litter horizons are from Kopáček *et al.* (2002a, 2002b) and were also determined by identical methods.

## Decomposition of cellulose

Cumulative decomposition activity of the forest floor was measured according to Kurka (2001) at plots PL-LS, PL-HN, CT-L, and CT-H from June 2003 to May 2013. Cellulose strips (filter paper, 16 × 9 cm, weight of ~1.0 g, 10 replicates at each plot) were inserted into the litter horizon (3–5 cm below its surface) in string bags (polyethylene, mesh opening of 1.5 mm) and exposed for periods lasting 1–3 months in summer and ~6 months in winter. After the exposure, bags were removed and replaced by new ones in the same places. In the laboratory, the remaining cellulose was air dried and, after removal of soil particles, roots and debris, loss on ignition was determined by combustion at 550 °C for 4 hours. The differences between the losses on ignition of the original cellulose strips (average for 5 replicates) and the remaining cellulose in the individual bags after the field exposure were used to determine the cumulative cellulose decomposition. In this study, we used average values calculated for all 10 replicates at each plot during sampling periods identical to those of the litter sampling, i.e. November–May for winter and June–October for summer. Results are expressed in mol of mineralized C ( $0.037 \text{ mol g}^{-1} \text{ cellulose}$ )  $\text{m}^{-2} \text{ day}^{-1}$ .

## Data evaluation and statistics

Average fluxes ( $F_{e,i}$ ;  $\text{mol m}^{-2} \text{ day}^{-1}$  for elements

and  $\text{g m}^{-2} \text{ day}^{-1}$  for ash) of a constituent  $e$  in litter category  $i$  (needles, twigs, bark, lichen, cones, beech leaves, birch and rowan leaves and twigs, and "other material") were calculated for each plot and period as:

$$F_{e,i} = m_i c_{e,i} / d \quad (1)$$

where  $m_i$  ( $\text{g m}^{-2} \text{ period}^{-1}$ ) is the DW amount of litter category  $i$  during the sampling period,  $d$  ( $\text{day period}^{-1}$ ) is the length of the period, and  $c_{e,i}$  ( $\text{mol g}^{-1}$  for elements and  $\text{g g}^{-1}$  for ash) is the concentration of constituent  $e$  in the litter category  $i$ . The average composition ( $c_e$ ,  $\text{mol g}^{-1}$ ) of total litterfall (all categories) was then calculated for each plot and sampling period as a mass-weighted mean for all litter categories as follows:

$$c_e = \Sigma F_{e,i} / \Sigma m_i \quad (2)$$

For the purpose of this study, the average chemical composition of individual litter categories beneath living trees in the PL and CT catchments was the arithmetical mean of all available  $c_{e,i}$  values, calculated for plots of similar forest age and health. Thus, the average composition of total litter, needles, twigs, bark, lichen, cones, and "other material" was based on all 20 samplings at both CT plots ( $n = 40$ ) for the CT catchment, but only on the PL-LS, PL-HS, and PL-HN plots prior their infestation in the PL catchment ( $n = 17$ ). Data on spruce litter from the PL-LN plot, with a contribution of young trees, were not included in these averages. In contrast, the average composition of beech, birch, and rowan leaves and birch and rowan twigs was calculated as the arithmetical mean for all plots where they occurred, including PL-LN.

Trends in chemical composition and amount of individual litter categories were based on annual averages in the CT catchment and calculated on a calendar year basis ( $n = 4$ ; 2 seasons and 2 plots). In contrast, chemical changes in litter composition were evaluated with respect to the time of plot infestation in the PL catchment. Thus, year  $-1$  represents litter chemistry prior to infestation ( $n = 6$ ), year 0 represents bark-beetle infestation and tree death ( $n = 6$ ), and the following years 1–8 refer to the age of dead trees ( $n = 2$ –6), regardless of calendar

years. Presence of increasing or decreasing trend in chemistry of individual litter categories was tested using a non-parametric Mann-Kendall test (Hipel and McLeod 1994). If a significant trend was detected and if the requirements for its description using a linear model were met, we quantified the rate of increase or decrease using the slope of fitted linear model. The slope values were calculated using a linear regression of annual average concentrations against time over the study period, i.e. during 2004–2013 and from  $-1$  to 8 for the CT and PL catchments, respectively ( $n = 10$ , except for needle and cone at the PL plots, with  $n = 5$ ).

Significances of differences between element concentrations in living tissue and litter needles, twigs, and bark during forest decay were tested using a non-parametric Mann-Whitney- $U$  test in STATISTICA ver. 9. A non-parametric procedure was used because of non-normal data distribution (Kolmogorov-Smirnov test, STATISTICA ver. 9).

Presence of increasing or decreasing trend in decomposition rate of cellulose (with two periods in each year) was tested using a Mann-Kendall test (Hipel and McLeod 1994).

## Results

### Litterfall

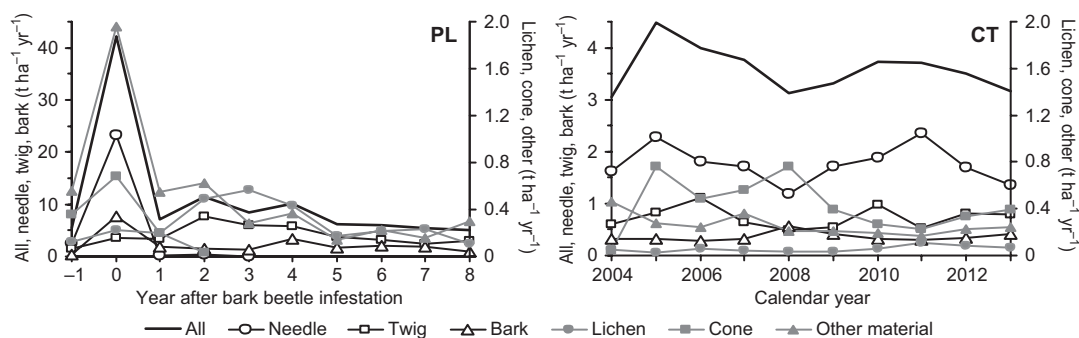
The chemical composition of individual litter categories beneath living trees exhibited similar differences across both catchments (Table 2). The ratios between element concentrations in the identical litter categories observed in the PL and CT catchments (PL:CT) varied only in a relatively narrow range, from PL:CT of 0.7 for Al in cones to 1.3 for ash in needles. The most important between-catchment difference was in  $\sim 20\%$  higher Ca concentrations in total litterfall beneath the uninfested trees in the PL than CT catchments (Table 2), resulting from different bedrock composition and higher base saturation of the PL soils (Kopáček *et al.* 2002a, 2002b, 2010). In contrast to the relatively small between-catchment differences, much greater differences occurred between chemical compositions of individual litter categories at each plot



**Table 2.** Average ( $\pm$  SD;  $n$  = number of observations) chemical composition of litter beneath living trees in the catchments of Plešné (PL) and Čertovo (CT) lakes.

	<i>n</i>	Ash (mg g <sup>-1</sup> )	C (mmol g <sup>-1</sup> )	N (mmol g <sup>-1</sup> )	P ( $\mu$ mol g <sup>-1</sup> )	Ca ( $\mu$ mol g <sup>-1</sup> )	Mg ( $\mu$ mol g <sup>-1</sup> )	Na ( $\mu$ mol g <sup>-1</sup> )	K ( $\mu$ mol g <sup>-1</sup> )	Al ( $\mu$ mol g <sup>-1</sup> )	Fe ( $\mu$ mol g <sup>-1</sup> )	Mn ( $\mu$ mol g <sup>-1</sup> )
Total spruce litter <sup>1</sup>	17	27 $\pm$ 4	44 $\pm$ 0.5	0.83 $\pm$ 0.09	22 $\pm$ 3	85 $\pm$ 9	16 $\pm$ 3	3 $\pm$ 0.7	31 $\pm$ 6	19 $\pm$ 7	7 $\pm$ 3	4 $\pm$ 1.1
Needles	40	22 $\pm$ 3	44 $\pm$ 0.7	0.84 $\pm$ 0.12	23 $\pm$ 4	71 $\pm$ 11	16 $\pm$ 2	3 $\pm$ 0.8	32 $\pm$ 6	15 $\pm$ 7	5 $\pm$ 2	3 $\pm$ 0.6
	17	33 $\pm$ 4	44 $\pm$ 0.5	0.79 $\pm$ 0.09	22 $\pm$ 3	90 $\pm$ 10	16 $\pm$ 2	1 $\pm$ 0.4	31 $\pm$ 8	4 $\pm$ 1	1 $\pm$ 0.3	6 $\pm$ 1.7
	40	25 $\pm$ 3	44 $\pm$ 0.8	0.86 $\pm$ 0.09	24 $\pm$ 5	77 $\pm$ 11	15 $\pm$ 3	1 $\pm$ 0.5	30 $\pm$ 9	5 $\pm$ 1	1 $\pm$ 0.4	5 $\pm$ 0.4
Twigs	17	15 $\pm$ 2	45 $\pm$ 0.9	0.68 $\pm$ 0.09	16 $\pm$ 2	73 $\pm$ 10	11 $\pm$ 3	2 $\pm$ 0.4	17 $\pm$ 3	20 $\pm$ 4	7 $\pm$ 1	2 $\pm$ 0.4
	40	14 $\pm$ 2	45 $\pm$ 0.8	0.72 $\pm$ 0.10	17 $\pm$ 3	69 $\pm$ 9	11 $\pm$ 2	2 $\pm$ 0.8	17 $\pm$ 3	18 $\pm$ 4	6 $\pm$ 2	2 $\pm$ 0.3
Bark	17	33 $\pm$ 4	43 $\pm$ 0.5	0.77 $\pm$ 0.13	16 $\pm$ 3	185 $\pm$ 32	16 $\pm$ 5	4 $\pm$ 1.1	20 $\pm$ 3	31 $\pm$ 7	11 $\pm$ 3	4 $\pm$ 0.6
	40	28 $\pm$ 4	44 $\pm$ 0.9	0.83 $\pm$ 0.19	18 $\pm$ 3	164 $\pm$ 34	16 $\pm$ 2	3 $\pm$ 0.9	19 $\pm$ 4	28 $\pm$ 7	9 $\pm$ 3	4 $\pm$ 0.4
Lichen	17	26 $\pm$ 5	41 $\pm$ 0.5	1.53 $\pm$ 0.10	22 $\pm$ 2	82 $\pm$ 25	23 $\pm$ 3	5 $\pm$ 1.0	66 $\pm$ 5	38 $\pm$ 9	14 $\pm$ 3	2 $\pm$ 0.6
	40	28 $\pm$ 4	41 $\pm$ 0.7	1.45 $\pm$ 0.11	25 $\pm$ 4	107 $\pm$ 41	24 $\pm$ 3	5 $\pm$ 1.5	65 $\pm$ 6	38 $\pm$ 9	13 $\pm$ 3	3 $\pm$ 0.5
Cone	10	7 $\pm$ 3	44 $\pm$ 1.0	0.63 $\pm$ 0.61	18 $\pm$ 17	9 $\pm$ 8	20 $\pm$ 12	2 $\pm$ 1.5	53 $\pm$ 22	2 $\pm$ 1	1 $\pm$ 0.6	1 $\pm$ 0.6
	34	9 $\pm$ 5	44 $\pm$ 1.1	0.54 $\pm$ 0.31	18 $\pm$ 11	8 $\pm$ 5	20 $\pm$ 7	2 $\pm$ 1.3	59 $\pm$ 26	3 $\pm$ 1	1 $\pm$ 0.5	1 $\pm$ 0.3
Other material	17	40 $\pm$ 6	43 $\pm$ 0.7	1.48 $\pm$ 0.13	41 $\pm$ 5	82 $\pm$ 14	26 $\pm$ 6	13 $\pm$ 4	47 $\pm$ 7	79 $\pm$ 19	28 $\pm$ 8	3 $\pm$ 0.8
	40	36 $\pm$ 11	43 $\pm$ 1.2	1.47 $\pm$ 0.22	43 $\pm$ 9	70 $\pm$ 13	25 $\pm$ 5	11 $\pm$ 6	45 $\pm$ 9	74 $\pm$ 32	26 $\pm$ 9	3 $\pm$ 0.5
Beech leaves	17	39 $\pm$ 8	44 $\pm$ 0.9	1.21 $\pm$ 0.24	27 $\pm$ 9	54 $\pm$ 9	22 $\pm$ 4	3 $\pm$ 0.9	49 $\pm$ 21	8 $\pm$ 4	4 $\pm$ 1	3 $\pm$ 0.6
Birch leaves	7	26 $\pm$ 2	45 $\pm$ 0.9	1.55 $\pm$ 0.30	45 $\pm$ 10	126 $\pm$ 38	29 $\pm$ 4	3 $\pm$ 1.2	73 $\pm$ 23	13 $\pm$ 9	5 $\pm$ 3	9 $\pm$ 4
Birch twigs	6	15 $\pm$ 2	46 $\pm$ 0.6	0.81 $\pm$ 0.16	23 $\pm$ 5	100 $\pm$ 22	25 $\pm$ 9	2 $\pm$ 1	34 $\pm$ 14	4 $\pm$ 4	2 $\pm$ 2	4 $\pm$ 2
Rowan leaves	14	39 $\pm$ 4	45 $\pm$ 0.7	1.49 $\pm$ 0.27	45 $\pm$ 8	236 $\pm$ 52	60 $\pm$ 20	3 $\pm$ 1.7	55 $\pm$ 16	13 $\pm$ 9	5 $\pm$ 3	16 $\pm$ 7
Rowan twigs	9	44 $\pm$ 9	41 $\pm$ 1.1	0.60 $\pm$ 0.10	19 $\pm$ 3	308 $\pm$ 57	60 $\pm$ 24	2 $\pm$ 0.8	53 $\pm$ 25	5 $\pm$ 1	2 $\pm$ 2	11 $\pm$ 5

<sup>1</sup> Total spruce litter: the average composition of litterfall calculated for all spruce litter categories (needles, twigs, bark, lichen, cone, and other material) from Eqs. 1 and 2.<sup>2</sup> Averages for plots CT-L and CT-H in the CT catchment; and PL-LS, PL-HS, and PL-HN prior to their infestation in the PL catchment.<sup>3</sup> Average composition at the CT-L plot.<sup>4</sup> Average composition at the PL-LN plot.<sup>5</sup> Average for plots PL-LN and PL-HN.



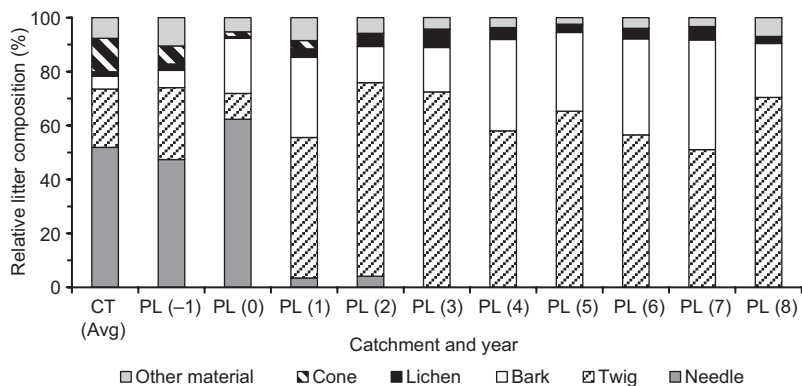
**Fig. 3.** Annual fluxes of spruce litter in the Plešné (PL) catchment (averages for plots PL-LS, PL-HS, and PL-HN) prior to bark-beetle infestation (year -1), during the infestation (year 0), and after the infestation (dead trees; years 1–8), and in the Čertovo (CT) catchment (averages for plots CT-L and CT-H). “All” represents the sum of all litter categories including rowan. The category “other material” refers to remaining material, consisting mostly of poorly identifiable fragments.

(Table 2). The lowest concentrations of (i) ash, N, Ca, Al, Fe, and Mn were in cones, (ii) Mg and K in twigs, (iii) P in twigs and bark, and (iv) C in lichen. The highest concentrations of ash were in rowan litter and in “other material”. “Other material” also exhibited high concentrations of N and P, and the maximum concentrations of Na, Al, and Fe. Birch leaves and rowan leaves and twigs were rich in N, P, and Mn. The rowan litter had the highest concentrations of Ca and Mg, which were even higher than in bark (Table 2). The ratios between maximum and minimum concentrations of elements in the litter categories varied within one to two orders of magnitude, with the minimum ratio for C (1.1) and the maximum ratios of 18–41 for Ca, Al, Fe, and Mn. “Other material” had ~40 times higher Al and Fe concentrations than lichen, and rowan leaves and twigs had 28 and 37 times higher Ca concentrations than cones, respectively. Consequently, the chemical composition of total litterfall at the PL and CT plots reflected mainly the relative contribution of individual litter categories to the total litterfall, while the between-catchment differences in litter composition were less important.

Total litterfall was only slightly higher at the PL plots prior to bark-beetle infestation than the 2004–2013 average for the CT catchment ( $5.4$  vs.  $3.6 \pm 0.4$  t ha<sup>-1</sup> yr<sup>-1</sup>; Fig. 3), and the relative contribution of individual spruce litter categories was similar in both catchments (i.e., 49% needles, 24% twigs, 10% cones, 9% “other material”, 6% bark, and 2% lichen on average;

Fig. 4). The litterfall flux as well as the relative contribution of individual litter categories remained relatively stable in the CT catchment during 2004–2013, with coefficients of variation varying from 12% for the total litter to 54% for cones. In contrast, the litterfall flux and relative contribution of individual litter categories dramatically changed in the PL catchment (Figs. 3 and 4). Bark-beetle infestation of the PL forest resulted in one order of magnitude higher litterfall ( $42$  t ha<sup>-1</sup> yr<sup>-1</sup>) in the year of forest dieback (year 0) than prior to infestation (year -1). This litterfall flux was dominated by needles (62%,  $23$  t ha<sup>-1</sup> yr<sup>-1</sup>), with a large proportion of green, non-senescent needles, and bark (20%,  $7.6$  t ha<sup>-1</sup> yr<sup>-1</sup>). In the following 8 years, the total litterfall was dominated by twigs (and small branches) and bark (on average 62% and 27%, respectively), while the contribution of needles and cones rapidly declined and became negligible from the 3rd year after infestation. The respective fluxes of twigs and lichen continuously increased from 1.4 to  $7.7$  t ha<sup>-1</sup> yr<sup>-1</sup> and from 0.13 to  $0.57$  t ha<sup>-1</sup> yr<sup>-1</sup> between years -1 and 3, and then decreased to ~3 t ha<sup>-1</sup> yr<sup>-1</sup> and  $0.11$  t ha<sup>-1</sup> yr<sup>-1</sup> in year 8 after infestation. The relative contribution of litter categories to the total litterfall was relatively stable during 4–8 years after infestation, but its total flux further decreased to 5–10 t ha<sup>-1</sup> yr<sup>-1</sup>, because some of the dead trees were already broken by winds and canopies of the remaining trees became thinner. But, even at the end of this study in 2013 the total litterfall from the remaining





**Fig. 4.** Relative contributions of the major litter categories in the total spruce litterfall in the Čertovo (CT) catchment (average for plots CT-L and CT-H during June 2003–May 2013) and in the Plešné (PL) catchment (averages for plots PL-LS, PL-HS, and PL-HN) prior to bark-beetle infestation (year –1), during the infestation (year 0), and after the infestation (dead trees; years 1–8). The category “other material” refers to remaining material, consisting mostly of poorly identifiable fragments.

dead trees was higher in the PL catchment than in the uninfested CT plots (5.0 vs. 3.2 t ha<sup>-1</sup> yr<sup>-1</sup>; Fig. 3).

Changes in the litterfall flux following bark-beetle infestation affected nutrient inputs to the forest floor. The nutrient fluxes associated with annual average litterfall prior to bark-beetle infestation represented 5%–17% of their pools in the PL litter horizon, with the minimum value for K and maximum for Mn (Table 3). This flux abruptly increased to 15%–36% for N, K, P, C

and Mg, and even to 61% for Mn and 70% for Ca (Table 3) during the first year of forest infestation, and resulted in a pronounced enrichment of nutrients pools in the PL litter horizon. Even though nutrient inputs from litterfall decreased during the following 8 years, it still represented 3%–18% of the nutrient pools in the PL forest floor prior to forest infestation, and was thus similar to annual average nutrients inputs to the forest floor in the uninfested CT catchment (Table 3).

**Table 3.** Comparison of element pools in the litter horizon of the Plešné (PL) and Čertovo (CT) soils to their annual average fluxes in total litterfall including rowan.

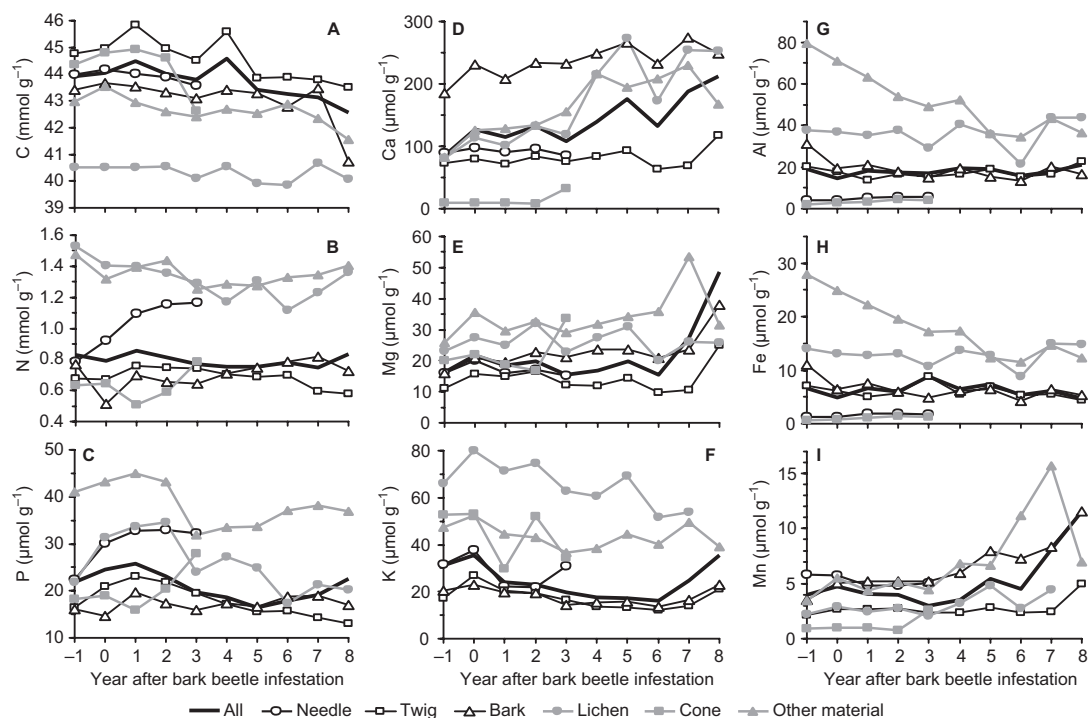
	Unit	C	N	P	Ca	Mg	K	Mn
<b>CT<sup>1</sup></b>								
Litter horizon <sup>2</sup>	mmol m <sup>-2</sup>	176731	6894	146	215	119	261	14
Litterfall (2004–2013)	mmol m <sup>-2</sup> yr <sup>-1</sup>	15042	283	8	24	5	11	1
	% <sup>4</sup>	8.5	4.1	5.2	11	4.5	4.2	8.3
<b>PL<sup>1</sup></b>								
Litter horizon <sup>3</sup>	mmol m <sup>-2</sup>	225131	7755	165	332	98	315	12
Litterfall (year –1)	mmol m <sup>-2</sup> yr <sup>-1</sup>	23530	444	12	45	9	17	2
	% <sup>4</sup>	11	5.7	7.1	14	8.8	5.3	17
Litterfall (year 0)	mmol m <sup>-2</sup> yr <sup>-1</sup>	69853	1182	37	232	36	53	8
	% <sup>4</sup>	31	15	23	70	36	17	61
Litterfall (years 1–8)	mmol m <sup>-2</sup> yr <sup>-1</sup>	18863	334	9	60	9	9	2
	% <sup>4</sup>	8.4	4.3	5.3	18.1	8.7	2.9	17.2

<sup>1</sup>) Averages for plots CT-L and CT-H in the CT catchment, and PL-LS, PL-HS, and PL-HN in the PL catchment.

<sup>2</sup>) Average element pools in the catchment of Čertovo Lake in 1997–2001 (Kopáček *et al.* 2002b).

<sup>3</sup>) Average element pools in the catchment of Plešné Lake in 1997–2001 (Kopáček *et al.* 2002a).

<sup>4</sup>) Contribution (%) of annual average element input in litterfall to its pool in the litter (O) horizon.



**Fig. 5.** Average concentrations of elements in the total litterfall (All) and major categories of spruce litter in the Plešné catchment (averages for plots PL-LS, PL-HS, and PL-HN) prior to bark-beetle infestation (year -1), during the infestation (year 0), and after the infestation (dead trees; years 1–8). Composition of total litterfall was calculated with Eqs. 1 and 2 for all litter categories including rowan. The category “other material” refers to remaining material, consisting mostly of poorly identifiable fragments.

## Trends in litterfall chemistry

Concentrations of all elements (except for Ca) remained stable in all litter categories in the reference CT catchment throughout the study, and exhibited only small year-to-year variability (*see* averages and the respective standard deviations; Table 2). The Ca concentrations, however, increased in the CT litter at both plots (with significant trends for all litter categories except for twigs and bark), with an average rate of  $2.5 \mu\text{mol Ca g}^{-1} \text{ yr}^{-1}$  ( $\tau = 0.64$ ,  $p = 0.012$ ) for the total litterfall.

In contrast, chemical composition of the PL litter categories changed during the study as follows: (1) Concentrations of C significantly decreased ( $\tau = -0.60$ ,  $p = 0.020$ ) in the total PL litterfall after bark-beetle infestation due mostly to their decreases in twigs ( $\tau = -0.56$ ,  $p = 0.032$ ) and “other material” ( $\tau = -0.64$ ,  $p = 0.012$ ), but also in needles and bark (Fig. 5A). (2) Concentrations of N were stable in the total litterfall, as

well as in most of litter categories, except for the PL needles, where they significantly increased ( $\tau = 1.00$ ,  $p = 0.028$ ) from  $0.79$  to  $1.17 \text{ mmol g}^{-1}$  between years -1 and 3, and the PL lichen, where they significantly decreased ( $\tau = -0.56$ ,  $p = 0.032$ ) from  $1.53$  to  $\sim 1.1$ – $1.3 \text{ mmol g}^{-1}$  during the study (Fig. 5B). (3) Concentrations of P increased in the total litterfall in the PL catchment between years -1 and 1, mainly due to increasing P concentrations in needles and their high proportion in the litterfall. Then, the contribution of needles to the total litterfall sharply decreased (Fig. 3) and P concentration in the total litterfall continuously decreased in parallel with its decrease in twigs (Fig. 5C), which formed the dominant litter category at that time (Fig. 4). Finally, P concentrations in the total PL litterfall started to increase in the last two years of the study, due to the occurrence of rowan litter, which is rich in P (Table 2). (4) Concentrations of Ca in the total litterfall increased significantly ( $\tau = 0.69$ ,  $p = 0.007$ ) in the PL catchment, similarly to the CT

catchment, but with a fourfold steeper slope ( $11 \mu\text{mol g}^{-1} \text{yr}^{-1}$ ) than in the CT catchment. These trends resulted from significant increases ( $\tau = 0.60$  to  $0.73$ ,  $p = 0.004$  to  $0.020$ ) in Ca concentrations in all litter categories except in twigs and bark (Fig. 5D). (5) In contrast to Ca, Mg concentrations did not exhibit any significant trend except for an increase ( $\tau = 0.64$ ,  $p = 0.012$ ) in the PL bark (Fig. 5E). Mg concentrations were relatively stable in the total PL litterfall 6 years after the forest dieback, but then started to increase during the last 2 years due to (i) steeply increasing concentrations in bark and twigs, and (ii) the contribution of rowan twigs and leaves to the total litterfall at the PL–HN plot. (6) Concentrations of K were decreasing 6 years after the forest dieback and then, similarly to Mg, increasing during the last 2 years in twigs and bark, and consequently, also in the total litterfall (Fig. 5F). (7) Concentrations of Al and Fe behaved similarly and were stable in most litter categories in the PL catchment throughout the study (Fig. 5G and H). One exception was significantly decreasing Al and Fe concentrations ( $4.7$  and  $1.7 \mu\text{mol g}^{-1} \text{yr}^{-1}$ , respectively;  $\tau = -0.78$ ,  $p = 0.002$  for both) in the PL “other material”. In contrast to mainly stable Al and Fe, Mn concentrations increased significantly in the PL bark ( $\tau = 0.91$ ,  $p = 0.0004$ ), lichen ( $\tau = 0.51$ ,  $p = 0.049$ ), and “other material” ( $\tau = 0.69$ ,  $p = 0.007$ ) (Fig. 5I). The increase in Mn concentrations in the total PL litterfall was especially steep in the last two years when rowan leaves and twigs rich in Mn (Table 2) contributed to the Mn flux in the PL catchment.

Needles shed in year 0 contained higher amounts of N and P than senescent needles in year  $-1$ , but lower than foliage (Table 4). The litter needles in year 0 had also higher concentrations of Al and Fe, but 19%–61% lower concentrations of K, Na, Mg, and Mn than foliage. Similar differences between the composition of living tissue and litter of infested trees in year 0 occurred also in the chemistry of twigs and bark, i.e. categories that (besides needles) were the highest contributors to the total litterfall (Fig. 3). The litter twigs and bark had lower concentrations of P, K, Na, Mg, and Mn, but higher concentrations of Al and Fe (and also Ca in litter twigs of age 0 and 1–8), than in living tissue (Table 4).

Changes in the chemistry and proportion of individual litter components after bark-beetle infestation affected some element ratios in the total litterfall in the infested vs. uninfested forests, while other ratios remained surprisingly stable despite significant concentration changes in individual components (Fig. 5). Most important trends in element ratios are summarized in Fig. 6. (1) C:N ratio: Concentrations of N in litter needles continuously increased at the infested plots (Fig. 5B), and even exceeded those in foliage in years 1 to 3 after the infestation (Table 4). N concentrations were steadily higher in litter bark, while  $\sim 35\%$  lower in the litter twigs than in living tissue. Despite changes in the chemistry of individual litter components, the C:N ratios and N concentration of total litterfall thus remained relatively stable in the infested PL forest (Fig. 6) because of the changing proportions of litter species. (2) N:P ratio: The stable N concentrations but changing P concentrations in the total PL litterfall affected N:P ratios after the forest infestations as follows: The N:P ratios continuously increased five years after infestation due to decreasing P concentrations in twigs (Fig. 5C), which dominated the litterfall at that time (Fig. 4). Then, N:P ratios started to decrease due to the increasing proportion of rowan litter, which is rich in P (Table 2). (3) N:Mg ratio: The N:Mg ratios were stable at the infested PL plots (similarly to the uninfested CT plots) 6 years after the forest dieback, but then started to decrease (Fig. 6) as a result of increasing Mg concentrations in bark and twigs (Fig. 5E) and the increasing contribution of rowan twigs and leaves with high Mg concentrations (Table 2) to the total litterfall. (4) Ca:Al ratio: The Ca:Al ratios of total litterfall increased in both study catchments due to increasing Ca concentrations in most litter categories (Fig. 5D), while Al concentrations were stable in the total litterfall (Fig. 5G).

### Cellulose decomposition

Decomposition rates of cellulose (a proxy for C mineralization rate) varied between  $2.1$  and  $20 \text{ mmol m}^{-2} \text{day}^{-1}$  and were expectedly higher in summer than in winter (Fig. 7). Besides the sea-

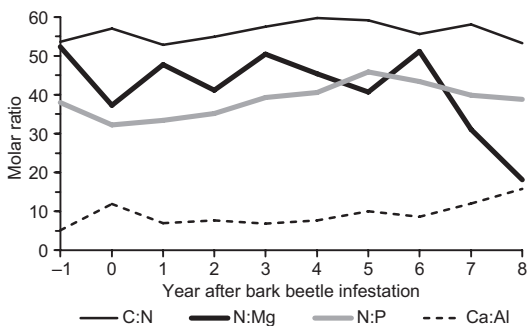
**Table 4.** Comparison of the composition of litterfall (LF) prior to, during, and after infestation, with the composition of Norway spruce foliage, twigs, and bark in the Plešné catchment (average for the PL-LS, PL-HS, and PL-HN plots). Different letters in superscripts indicate significant ( $p < 0.05$ ) differences among the tissue and litterfall categories.

$n$	Age <sup>1</sup>	C (mmol g <sup>-1</sup> )	N (mmol g <sup>-1</sup> )	P ( $\mu$ mol g <sup>-1</sup> )	Ca ( $\mu$ mol g <sup>-1</sup> )	Mg ( $\mu$ mol g <sup>-1</sup> )	Na ( $\mu$ mol g <sup>-1</sup> )	K ( $\mu$ mol g <sup>-1</sup> )	Al ( $\mu$ mol g <sup>-1</sup> )	Fe ( $\mu$ mol g <sup>-1</sup> )	Mn ( $\mu$ mol g <sup>-1</sup> )	Molar ratio	
												C:N	C:P
Foliage <sup>2</sup>	45	43.1 <sup>a</sup>	0.96 <sup>b</sup>	37 <sup>c</sup>	81	31 <sup>b</sup>	1.7 <sup>b</sup>	97 <sup>c</sup>	2.8 <sup>b</sup>	1.1 <sup>a</sup>	8.9 <sup>b</sup>	45 <sup>ab</sup>	1160 <sup>a</sup>
LF-needles	6	44.0 <sup>b</sup>	0.79 <sup>a</sup>	22 <sup>a</sup>	90	16 <sup>a</sup>	0.8 <sup>a</sup>	31 <sup>ab</sup>	4.1 <sup>b</sup>	1.2 <sup>a</sup>	5.8 <sup>a</sup>	56 <sup>c</sup>	1960 <sup>c</sup>
LF-needles	6	44.2 <sup>b</sup>	0.92 <sup>b</sup>	30 <sup>b</sup>	98	20 <sup>a</sup>	1.1 <sup>ab</sup>	38 <sup>b</sup>	4.2 <sup>bc</sup>	1.3 <sup>a</sup>	5.7 <sup>a</sup>	48 <sup>b</sup>	1470 <sup>b</sup>
LF-needles	16	43.8 <sup>b</sup>	1.14 <sup>c</sup>	33 <sup>bc</sup>	90	16 <sup>a</sup>	1.7 <sup>b</sup>	25 <sup>a</sup>	5.6 <sup>c</sup>	1.9 <sup>b</sup>	4.9 <sup>a</sup>	38 <sup>a</sup>	1340 <sup>ab</sup>
Twigs <sup>2</sup>	9	44.2 <sup>a</sup>	1.01 <sup>b</sup>	45 <sup>b</sup>	77	33 <sup>c</sup>	5.0 <sup>b</sup>	97 <sup>c</sup>	15 <sup>a</sup>	4.8 <sup>a</sup>	5.7 <sup>b</sup>	44 <sup>a</sup>	980 <sup>a</sup>
LF-twigs	6	44.8 <sup>ab</sup>	0.68 <sup>a</sup>	16 <sup>a</sup>	73	11 <sup>a</sup>	2.2 <sup>a</sup>	17 <sup>a</sup>	20 <sup>b</sup>	7.1 <sup>b</sup>	2.2 <sup>a</sup>	66 <sup>b</sup>	2710 <sup>b</sup>
LF-twigs	6	45.0 <sup>b</sup>	0.67 <sup>a</sup>	21 <sup>a</sup>	79	16 <sup>b</sup>	2.6 <sup>a</sup>	27 <sup>b</sup>	18 <sup>ab</sup>	6.1 <sup>ab</sup>	2.7 <sup>a</sup>	67 <sup>b</sup>	2150 <sup>b</sup>
LF-twigs	35	44.5 <sup>ab</sup>	0.69 <sup>a</sup>	18 <sup>a</sup>	82	14 <sup>b</sup>	2.5 <sup>a</sup>	16 <sup>a</sup>	17 <sup>ab</sup>	5.9 <sup>ab</sup>	2.9 <sup>a</sup>	65 <sup>b</sup>	2540 <sup>b</sup>
Bark <sup>2</sup>	24	41.3 <sup>a</sup>	0.49 <sup>a</sup>	22 <sup>c</sup>	203 <sup>a</sup>	37 <sup>c</sup>	4.0 <sup>b</sup>	68 <sup>c</sup>	4.9 <sup>a</sup>	1.5 <sup>a</sup>	8.8 <sup>c</sup>	84 <sup>b</sup>	1910 <sup>a</sup>
LF-bark	6	43.4 <sup>b</sup>	0.77 <sup>b</sup>	16 <sup>ab</sup>	185 <sup>a</sup>	16 <sup>a</sup>	3.6 <sup>b</sup>	20 <sup>b</sup>	31 <sup>c</sup>	11 <sup>c</sup>	3.5 <sup>a</sup>	56 <sup>a</sup>	2690 <sup>bc</sup>
LF-bark	6	43.7 <sup>b</sup>	0.51 <sup>a</sup>	15 <sup>a</sup>	231 <sup>b</sup>	21 <sup>ab</sup>	2.3 <sup>a</sup>	23 <sup>b</sup>	20 <sup>b</sup>	6.5 <sup>b</sup>	5.0 <sup>b</sup>	85 <sup>b</sup>	2960 <sup>c</sup>
LF-bark	35	43.0 <sup>b</sup>	0.72 <sup>b</sup>	18 <sup>b</sup>	243 <sup>b</sup>	24 <sup>b</sup>	2.6 <sup>a</sup>	17 <sup>a</sup>	17 <sup>b</sup>	5.9 <sup>b</sup>	7.1 <sup>bc</sup>	59 <sup>a</sup>	2430 <sup>b</sup>

<sup>1</sup> Litter age: -1 = one year prior to infestation; 0 = the year of infestation; 1–3 and 1–8 = averages for 3 and 8 years after infestation, respectively. The 1–8 age category also includes rowan litter.

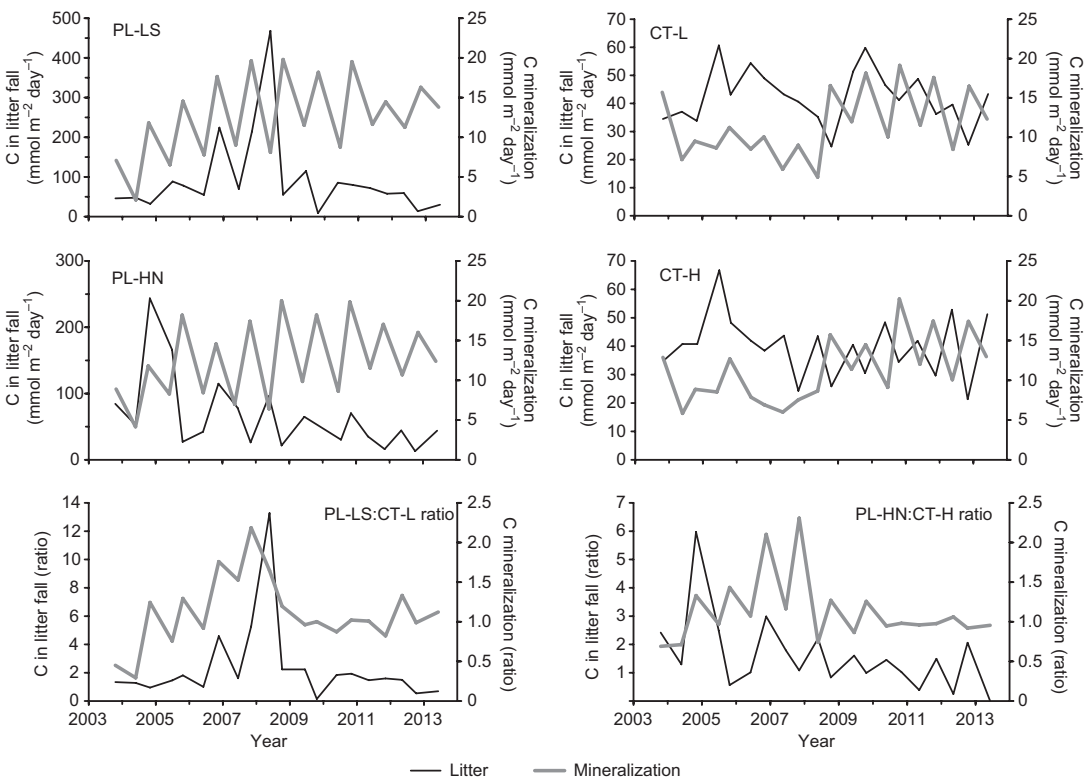
<sup>2</sup> Data are from Kopáček et al. (2010) and Svoboda et al. (2006b) and refer to the composition of fresh Norway spruce tissue prior to bark-beetle infestation.

sonal variability, the rates significantly increased at all plots during the study: PL-LS ( $\tau = 0.57$ ,  $p = 0.001$ ), PL-HN ( $\tau = 0.50$ ,  $p = 0.004$ ), CT-L ( $\tau = 0.36$ ,  $p = 0.043$ ), and CT-H ( $\tau = 0.61$ ,  $p = 0.001$ ). The trends in cellulose decomposition rates, however, differed between the catchments. The increasing trends at the CT plots were caused by generally higher rates of decomposition during 2008–2013 than during 2003–2007, despite the relatively stable C input in litterfall. In contrast, cellulose decomposition rates increased continuously with the increasing litterfall at the PL plots, and then remained high till the end of study (Fig. 7). Ratios between cellulose decomposition rates at the PL and CT plots of similar elevations (i.e., PL-LS vs. CT-L and PL-HN vs. CT-H) were below 1 at the beginning of the study, because decomposition rate was higher at the CT than PL plots. However, the ratios increased after the bark-beetle outbreak and elevated litterfall to values  $\sim 2$ , and then stabilized around 1 during



**Fig. 6.** Time series of molar ratios between element fluxes in the total litterfall (sum of all litter categories including rowan) in the Plešné catchment (averages for plots PL-LS, PL-HS, and PL-HN) prior to bark-beetle infestation (year -1), during the infestation (year 0), and after the infestation (dead trees; years 1–8).

2008–2013 (Fig. 7, lower panel), indicating similar cellulose decomposition rates in both catchments during this period.



**Fig. 7.** Carbon (C) in total litterfall and cellulose decomposition (expressed as C mineralization) at the studied plots in the catchments of Plešné and Čertovo Lakes. The lower panels show ratios between C litterfall and cellulose decomposition at the PL and CT sites of similar elevation (L, low; H, high). For site abbreviations see Table 1.

## Discussion

### Effects of bark-beetle infestation on litterfall composition and flux

Forest infestation by bark beetle and the following dieback of mature Norway spruce stands caused pronounced changes in both litterfall flux and composition. The dead trees lost most needles and cones within a year after the outbreak. Then, they continuously lost twigs, bark, and branches until the end of this study. Surprisingly, litterfall flux was relatively high (similar to that at uninfested plots) as late as 8 years after the bark-beetle outbreak (Fig. 3). Even though the composition of litterfall changed during the years following forest infestation due to the absence of needles and cones in the progressed stage of forest decay, it still represented an important input of elements to the forest floor almost one decade after the bark-beetle outbreak.

Retranslocation (nutrient recovery from senescent tissues) is an important mechanism for the conservation of nutrients within a tree (Miller 1995). Spruce trees clearly remobilize nutrients from old foliage to new needles (Bauer *et al.* 1997). The fast dieback of infected trees resulted in low nutrient remobilization, and needles shed in the year of spruce dieback (year 0) had different composition from the foliage of the healthy canopies, but also from senescent needles fallen from healthy trees (year -1), which relocated part of the nutrients to living tissue (Table 4). Needles shed in year 0 contained higher amounts of N and P than senescent needles in year -1, but still lower N and P than foliage, confirming the low remobilization of nutrients in infected trees (Table 4). In the needles shed later after forest dieback (years 1–3), N concentrations increased and C:N (and also C:P) ratios decreased, probably indicating decay by endophytes already on the trees. Endophytic fungi have been shown to play an important role in decomposition (Korkama-Rajala *et al.* 2008). The litter depletion in K, Mg, and Mn as compared with their concentrations in living tissue (Table 4) probably occurred mostly in canopies, due to a partial washing off of these elements by precipitation (Kopáček *et al.* 2009). This process is responsible for high concentrations

of these elements in throughfall as compared with deposition in treeless areas (e.g., Pedersen and Bille-Hansen 1999, Kopáček *et al.* 2009). The long sampling intervals (on average six months in winter and three months in summer) during this study could, however, also partly underestimate litterfall fluxes of easily soluble elements, as observed elsewhere (Ukonmaanaho and Starr 2001). Many studies have shown that more mobile elements are easily leached from litter (e.g., Palviainen *et al.* 2004a, Berg and McClaugherty 2008), which is subjected to partial leaching during the residence time in the traps (Pedersen and Bille-Hansen 1999).

Calcium was the only element in this study exhibiting increasing trends in almost all litter categories in both catchments regardless of the forest health. This Ca increase could reflect an increasing base saturation of soils in both catchments between 2000 and 2010 (J. Kaňa unpubl. data) due to continuously decreasing terrestrial losses of base cations. This decline in leaching of base cations (mostly Ca) clearly accompanies the decreasing leaching of strong acid anions during the recovery of the CT and PL catchments from acidification (Majer *et al.* 2003, Oulehle *et al.* 2013). The lower Ca leaching from soils thus probably caused its increasing availability for plants and increasing concentrations in tree tissues. The long-term continuously increasing Ca concentrations in the PL litter after the forest infestation (Fig. 5D) was, however, surprising. We expected stable or slightly decreasing Ca concentrations in the litterfall from the dead trees. Such a trend would correspond with general changes in the chemical composition of spruce litter during the early phase of its decay, with decreasing concentrations of K, Mn, and Mg, increasing Al and Fe concentrations, and minor changes in Ca and N concentrations (Palviainen *et al.* 2004a, Berg and McClaugherty 2008). While concentrations of other elements mostly behaved in concordance with these general patterns, concentrations of Ca significantly increased. The question why these changes in Ca concentrations in the litterfall from dead canopies differed from that generally occurring in decaying litter on the forest floor (Berg and McClaugherty 2008) remains, however, unexplained.



## Effects of bark-beetle infestation on cellulose decomposition and soil element pools and leaching

The elevated nutrient input to forest floor of infested plots (Table 3) and changing microclimatic conditions [soil temperature (Hais and Kučera 2008) and moisture (Mikkelsen *et al.* 2013a)] probably contributed to the elevated cellulose decomposition rate at the PL plots (Fig. 7). But, the change in cellulose decomposition following the higher input in litterfall was not straightforward. Even though the forest dieback was followed by an abrupt increase in litter inputs and increasing soil temperature (Hais and Kučera 2008), the increase in decomposition of cellulose inserted in the litter layer was relatively slow (Fig. 7). The probable explanation for this pattern is slow decomposition of and nutrient release from the litter above cellulose strips, supporting development of cellulose decaying microflora. The composition of the total litterfall was dominated by needles, twigs, and branches, i.e., the material high in lignin and relatively low in nutrient concentrations. The mineralization rate of litter is influenced by its initial composition, with low decomposition rates usually connected with high concentrations of lignin and phenolic compounds, and with low P and N availability (Aber and Mellilo 1982, Wardle *et al.* 2003, Šantrůčková *et al.* 2006). Slightly higher nutrient concentrations in needles, bark, and twigs just after tree dieback (Table 4) thus probably supported cellulose decomposition, but likely only until easily available nutrients were depleted again, i.e. during the following several years. The elevated cellulose decomposition rates, persisting at the PL plots until the end of our study, can be then probably attributed to (i) the development of understory vegetation, including grasses (K. Matějka pers. comm.), which are more rich in nutrients and have lower concentrations of lignin and phenolics than spruce litter (Wardle *et al.* 2003, Šantrůčková *et al.* 2006, Bárta *et al.* 2010), and (ii) the higher soil temperature and moisture (Hais and Kučera 2008, Mikkelsen *et al.* 2013a).

Our method based on cellulose decomposition can be used only to track relative changes between the plots, but does not enable a quan-

tification of C mineralization rates in the whole litter horizon. Data presented in Fig. 7 thus refer only to mineralization rates in a thin layer 3–5 cm below the forest floor, where the cellulose was inserted. The changes in C mineralization rates in the uppermost layers of litter horizon could probably be greater than that reflected by our results, due to higher enrichment of the forest floor with nutrients (Table 3). The release of available nutrients from decaying litter is slow (Šantrůčková *et al.* 2006) and their transport to deeper horizons is probably minor. In addition, elevated temperature on the soil surface compared to deeper soil layers could also enhance the C mineralization rate in the upper layer of the litter horizon.

Forest dieback temporally alters surface water composition in affected areas (Likens and Bormann 1995, Oulehle *et al.* 2013, Vrba *et al.* 2013). The elevated nutrient input in litterfall and mineralization (Fig. 7), nutrient release from the litter at the early stages of decay as observed elsewhere (Palviainen *et al.* 2004a, 2004b), and decreased nutrient uptake by the attacked forest resulted in sharply elevated terrestrial exports of nitrate and base cations in the PL catchment since 2004 (Kopáček *et al.* 2013b), analogous to the situation observed elsewhere after forest dieback or clearcuts (e.g., Huber *et al.* 2004b, McHale *et al.* 2007). The almost one order of magnitude higher litterfall after forest dieback than in uninfested Norway spruce stands (Fig. 3) represented an important increase in nutrient inputs into soils below the infested trees (Table 3). The litter decomposition increased soil concentrations of Ca, Mg, and K, which replaced Al and protons from the soil sorption complex and almost doubled the concentrations of exchangeable base cations in the uppermost soil horizons, as well as their base saturation (Kaňa *et al.* 2013). The elevated litterfall, reduced nutrient uptake by dead trees, and enhanced microbial mineralization (Tahovská *et al.* 2010) thus resulted in elevated leaching of nutrients to tributaries, but also importantly contributed to a recovery of the strongly acidified Bohemian Forest soils from long lasting atmospheric acidification (Kaňa *et al.* 2013, Kopáček *et al.* 2013b).

Our results on forest decay in unmanaged plots differ in several important aspects from

those observed in clear-cut areas. Even though the general patterns of ecosystem responses to forest disturbance are similar regardless the disturbance type, the intensity and duration of the responses differ between dieback by bark-beetle infestation in natural forests, windthrows in unmanaged forests and clear-cut plantations (Huber 2004a, 2004b, McHale *et al.* 2007). The major reasons for these differences include more biomass remaining on the unmanaged plots after natural dieback, longer-lasting nutrient inputs to soils from continuously decaying trees (Fig. 3), and the shading effect of standing dead trees, which mitigates changes in air and soil temperature (Hais and Kučera 2008, Turek *et al.* 2014). Moreover, as compared with windthrows, when most of the litter enters the forest floor abruptly and into relatively small patches where the trees lie, litterfall from infested trees distributes elements below tree canopies more evenly in both time and space (due to dispersion by wind). The longer-lasting litter inputs spread mineralization and nitrification over a longer time. Consequently, the amplitude of  $\text{NO}_3^-$  losses from soils is lower but has longer duration (7–8 years) after natural forest diebacks than after clear-cuts, when higher  $\text{NO}_3^-$  losses usually occur for a shorter period (3–5 years) (Cummins and Farrell 2003, Huber 2004a, Kopáček *et al.* 2013b). The characteristics of  $\text{NO}_3^-$  leaching are mimicked by the terrestrial export of Al, which to a large extent accompanies  $\text{NO}_3^-$  leaching (Mchale *et al.* 2007, Kopáček *et al.* 2013b). Consequently, the effect of Al on water biota is longer lasting but milder after natural forest diebacks than after clear-cuts.

Another important difference between unmanaged plots and clear-cut areas results from compositions of re-forestation stands. Natural re-forestation in unmanaged plots will have a higher proportion of deciduous trees, as was observed elsewhere in the Bohemian Forest. Jonášová and Prach (2004) and T. Zeppenfeld and R. Bače (pers. comm.) observed that there has been (besides spruce) a significant regeneration of rowan and, sporadically, beech in the naturally re-forestation stands, while the numbers of rowan were significantly lower in clear-cut areas. The rowan litter is richer in base cations and P (Table 2) and poorer in phenolic com-

pounds than any category of spruce litter (H. Šantrůčková unpubl. data). Consequently, rowan exhibits higher nutrient improvement capacities and higher nutrient return to the forest floor than other pioneer species (e.g. willow, birch) and effectively increases soil pH and base saturation compared to spruce forests (Emmer *et al.* 1998, Carnol and Bazgir 2013). The high Ca, Mg and K concentrations in rowan litter may be explained by the physiological characteristics of this plant leading to the better exploitation of soil resources from the total pool of available nutrients (Larcher 2003). The roots of rowan, as well as those of many other pioneer species, reach deeper soil horizons than spruce of similar age and export nutrients via litter from deeper soil horizons to the forest floor (Mauer and Palátová 2002, Puhe 2003). The presence of rowan in the naturally re-forestation plots will thus result in higher enrichment of the uppermost soil horizons with nutrients. High input of base cations in rowan litter will result in less acidic soils (as well as surface waters) during forest growth in naturally re-forestation unmanaged plots than in clear-cut areas artificially re-forested with spruce and beech (Hruška *et al.* 2002, Carnol and Bazgir 2013).

## Conclusion

The unmanaged PL forest was infested by the bark beetle in 2004–2008, and 88%–99% of spruce trees had died at the PL research plots by 2011. All dead trees were left in the PL catchment and there were no forest management. Total litterfall was only slightly higher in the PL plots prior to bark-beetle infestation than the 10-yr average for the uninfested CT catchment ( $5.4$  vs.  $3.6 \pm 0.4 \text{ t ha}^{-1} \text{ yr}^{-1}$ ), and the relative contributions of needles, twigs, cones, bark, lichen, and “other material” were similar in both catchments (i.e., 49%, 24%, 10%, 6%, 2%, and 9%, respectively). The flux of litterfall increased to  $42 \text{ t ha}^{-1} \text{ yr}^{-1}$  in the PL catchment after the bark-beetle infestation and remained higher than in the uninfested CT plots until the end of study ( $5.0$  vs.  $3.2 \text{ t ha}^{-1} \text{ yr}^{-1}$ ) despite the fact that > 52% of dead trees were already broken at the PL plots in 2013. The relative contribution of individual cat-

egories to the total litterfall changed after forest dieback from a dominance of needles (62%) and bark (20%) in the first year to a dominance of twigs (62%) and bark (27%) in the following 8 years. Litter from rowan trees occurred in the naturally-recovering PL-HN plot 6 years after the spruce forest dieback. The chemical composition of many PL litter categories changed, with the most pronounced trends in the total litterfall composition observed for C concentrations (decrease) and Ca concentrations (increase). In addition, concentrations of Mg, K, and P steeply increased in the total PL litterfall during the last two years of the study due to an increasing proportion of rowan litter, which is rich in nutrients. Compared with the original spruce stands, the natural regeneration of the affected PL plots with this pioneer tree thus contributes to a valuable enrichment of the uppermost soil horizons with nutrients. The elevated nutrient input in litterfall and possibly also changed microclimatic conditions (increased soil temperature and moisture) contributed to the elevated cellulose decomposition (a proxy for C mineralization rate) in the PL compared to the CT litter floor.

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